LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *NEASPLOTA AENIGMA* FRIEDBERG AND MATHIS (DIPTERA: TEPHRITIDAE) ON *ERIGERON DIVERGENS* TORREY AND GRAY (ASTERACEAE) IN SOUTHERN CALIFORNIA

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Abstract.—*Neaspilota aenigma* Freidberg and Mathis is a multivoltine, oligophagous fruit fly (Diptera: Tephritidae) developing in the flower heads of *Erigeron foliosus* Nuttall and *E. divergens* Torrey and Gray in the subtribe Asterinae of the tribe Astereae in southern California. This tephritid also has been reported in the southwestern United States bordering Mexico from five other genera and plant species belonging to the subtribe Solidagininae of the Astereae. The egg, first-, second-, and third-instar larvae, and puparium are described and figured. The dorsal sensory organ is well defined in all three instars. The caudal segment of the first and second instars is ringed by four stelex sensilla, but by six stelex sensilla in the third instar. In turn, each stelex sensillum in the first instar is ringed by several hemispherical, minute acanthae and one upright, apically rounded acanthus. The mouth hooks of the first and second instars are bidentate, but in the third instar are tridentate. The integumental petal is fused with the stomal sense organ in the first instar, but these structures are separate in the second instar. The ventrally-toothed oral ridges number seven or eight in the third instar, which compares to six oral ridges in three other congeners examined to date. All instars feed mainly on the ovules and soft achenes, but towards the end of the third stadium, the larva tunnels deeply into the receptacle, sometimes continuing through it into the pedicel. Pupariation occurs inside the mature flower heads, but no protective cell is formed, as with congeners that overwinter as a prepuparium. Instead, F_1 adults emerge from flower heads of desert shrubs in late spring (May) and early summer (June), mate, and complete a summer F_2 generation on late-flowering *E. divergens* growing at higher elevations along with *E. foliosus* (July–August) and a fall F_3 generation in different species of late-flowering desert shrubs (September–October). Some of these F_2 and probably all F_3 adults overwinter, and those that survive the winter aggregate the next spring (April–May) on preblossom host plants to mate and subsequently oviposit. *Pteromalus* sp. (Hymenoptera: Pteromalidae) and an unidentified species of Braconidae (Hymenoptera) are the principal parasitoids of *N. aenigma* in its *Erigeron* hosts.

Key Words: Insecta, *Neaspilota, Erigeron,* Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, oligophagy, seed predation, parasitoids

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Revision of the genus *Neaspilota* (Diptera: Tephritidae) by Freidberg and Mathis (1986) facilitated determination of specimens reared from California Asteraceae

(Goeden 1989) and stimulated several life-history studies, including those on *N. viridescens* Quisenberry (Goeden and Headrick 1992), *N. wilsoni* Blanc and Foote (Goeden and Headrick 1999), and *N. signifera* (Coquillett) (Goeden 2000). This paper describes the immature stages and life history of a fourth species from California, *Neaspilota aenigma* Freidberg and Mathis.

Materials and Methods

The present study was based in large part on dissections of flower heads of *Erigeron divergens* Torrey and Gray collected during 1996–1997 from the following locations in the northern section of the San Bernardino Nat. Forest, SW San Bernardino Co.: N of Grand View Point and just S of Big Bear Lake at 2190-m elevation; N of Wildhorse Spring at 2450 m; Serrano Meadows Picnic Area, N shore Big Bear Lake at 2020 m; and S of Staircase Canyon at 1690 m. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Ten first-, three second-, and 12 third-instar larvae, and seven puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbent cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied and photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Fifteen pairs of virgin males and females obtained from emergence cages also were held in each of 15 separate, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbent cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2000), Goeden et al. (1998a, b), Goeden and Headrick (1992, 1999), Goeden and Teerink (1997a, b, 1998, 1999a, b, c), Teerink and Goeden (1998, 1999), and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *N. aenigma* immature stages, adults, and parasitoids reside in my research collections.

Results and Discussion

Taxonomy

Adult.—*Neaspilota aenigma* was described by Freidberg and Mathis (1986, p. 32), who pictured the unpatterned wing, (p. 22) along with drawings (p. 33, Fig. 57–65) of the lateral aspect of the head, male right foretarsus, epandrium, distiphallus, epandrium and cerci, aculeus and its apex enlarged, and spermatheca.

Immature stages.—The egg, first-, second-, and third-instar larvae, and puparium heretofore have not been described or figured.

Egg: Only a single, intact egg (see Fig. 5A) was found and measured *in situ* within an immature, preblossom flower head. This egg was white, opaque, smooth, elongate-ellipsoidal, 0.7 mm long and 0.16 mm wide, tapered and smoothly rounded at both ends. Thus, the egg of *N. aenigma* could only be generally compared with the eggs of *N. viridescens* and *N. wilsoni* described in detail by Goeden and Headrick (1992, 1999).

First instar: White, elongate-cylindrical, bluntly rounded anteriorly and posteriorly (Fig. 1A); body segments well-defined, but apparently nearly free of minute acanthae; gnathocephalon smooth, lacking oral ridges (rugose pads), but with a pair of prominent integumental petals dorsal to mouth hooks (Fig. 1B-1, C-1, D-1, E-1); dorsal sensory organ a well-defined, dome-shaped papilla (Fig. 1B-2, C-2, D-2), pit sensillum on each side at base of dorsal sensory organ (Fig. 1D-3); anterior sensory lobe (Fig. 1B-3, C-3, D-4) bears the terminal sensory organ (Fig. 1B-4, D-5), pit sensory organ (Fig. 1D-6), lateral sensory organ (Fig. 1D-7), and supralateral sensory organ (Fig. 1D-8); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 1B-5, C-4, E-2), integumental petal (Fig. 1B-1, C-1, D-1, E-1) fused laterally with stomal sense organ (Fig. 1B-5, E-2); mouth hook bidentate (Fig. 1B-6, E-3); median oral lobe laterally flattened and ventrally ridged (Fig. 1B-7, E-4); verruciform sensillum dorsolaterad of dorsal sensory organ (Fig. 1C-5); meso- and metathoracic and abdominal lateral spiracular complexes not seen; caudal segment with two stelex sensilla, dorso- and ventrolaterad of posterior spiracular plates, each stelex sensillum basally ringed with two to three, hemispherical and one short, upright, apically rounded acanthae; posterior spiracular plate bears two ovoid rimae, ca. 0.005 mm in length (Fig. 1F-1), and four interspiracular processes, each with two to four branches, longest measuring ca. 0.008 mm (Fig. 1F-2); intermediate sensory complex with one stelex sensillum and one medusoid sensillum.

The first instar is similar in general habitus to that of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), and *N. signifera* (Goeden 2000). However, unlike *N. viridescens,* but like *N. wilsoni,* the dorsal sensory organ of the first instar of *N. aenigma* is well-defined (Fig. 1B-2, C-2, D-2), as is the anterior sensory lobe and integumental petal. Also, the pit sensory organ, not seen in *N. viridescens* (Goeden and Headrick 1992), is present in *N. aenigma* (Fig. 1D-6), as it is in *N. wilsoni* (Goeden and Headrick 1999). A fused integumental petal and stomal sense organ also was reported in first instars of *N. wilsoni* (Goeden and Headrick 1999) and *N. signifera* (Goeden 2000) as well as *Trupanea vicina* (Goeden and Teerink 1999b), but these structures were separated in *N. viridescens* (Goeden and Headrick 1992). Lateral stelex sensilla on the caudal segment that are basally ringed with upright acanthae also are found in *N. wilsoni* (Goeden and Headrick 1999), where the acanthae are more numerous and pointed, not solitary and rounded apically as in *N. aenigma.* The two stelex sensilla dorso- and ventrolaterad of the posterior spiracular plate in the first instar of *N. aenigma* agreed with the four such sensilla reported to ring the caudal segment of *N. wilsoni* (Goeden and Headrick 1999), but not the 10 sensilla reported to ring the caudal segment of *N. viridescens* (Goeden and Headrick 1992). The latter number may have included the four sensilla comprising the two intermediate sensory complexes.

Second instar: White, elongate-cylindrical, rounded anteriorly, truncated dorsoposteriorly (Fig. 2A), body segments well-defined, but apparently nearly free of minute acanthae; dorsal sensory organ not well-defined (Fig. 2C-1), with a single pore sensillum on inner side (Fig. 2C-2) and two pore sensilla on outer side at base (Fig. 2C-3); anterior sensory lobe (Fig. 2B-1, C-4) bears terminal sensory organ (Fig. 2B-2, C-5),
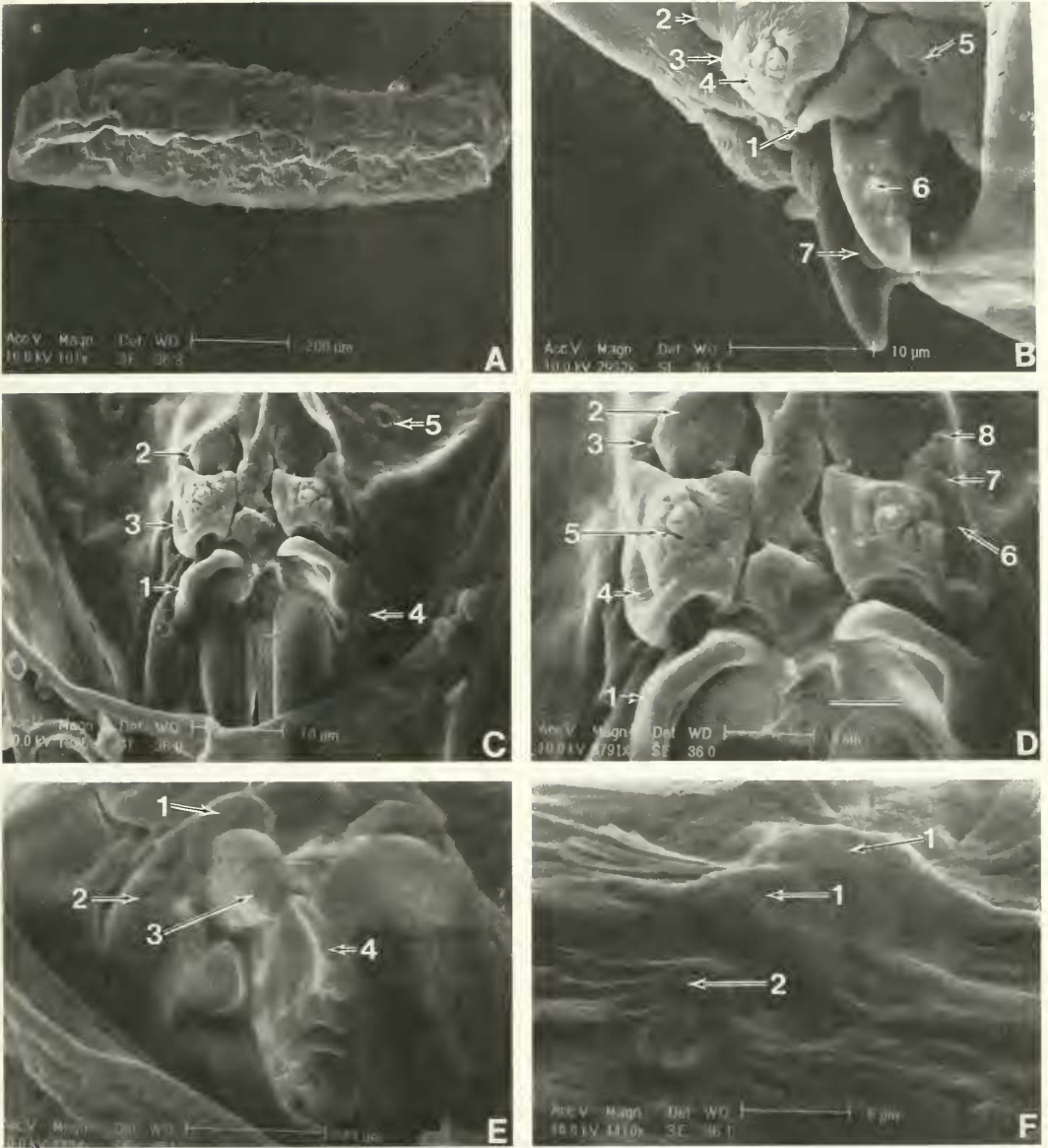
Fig. 1.   First instar of *Neaspilota aenigma:* (A) habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1- integumental petal, 2- dorsal sensory organ, 3- anterior sensory lobe, 4- terminal sensory organ, 5- stomal sense organ, 6- mouth hook, 7- median oral lobe; (C) gnathocephalon, frontal view, 1- integumental petal, 2- dorsal sensory organ, 3- anterior sensory lobe, 4- stomal sense organ, 5- verruciform sensillum; (D) gnathocephalon, enlarged frontal view, 1- integumental petal, 2- dorsal sensory organ, 3- pit sensillum, 4- anterior sensory lobe, 5- terminal sensory organ, 6- pit sensory organ, 7- lateral sensory organ, 8- supralateral sensory organ, (E) oral cavity, ventral view, 1- integumental petal, 2- stomal sense organ, 3- mouth hook, 4- median oral lobe, (F) posterior spiracular plate, 1- rima, 2- interspiracular process.

lateral sensory organ (Fig. 2B-3, C-6), supralateral sensory organ (Fig. 2B-4, C-7), and pit sensory organ (Fig. 2B-5, C-8); stomal sense organ present, but only partly viewed, ventrolaterad of anterior sensory lobe (Fig. 2C-9); mouth hook also not viewed in full (Fig. 2C-10); about eight papilliform, integumental petals dorsal to each
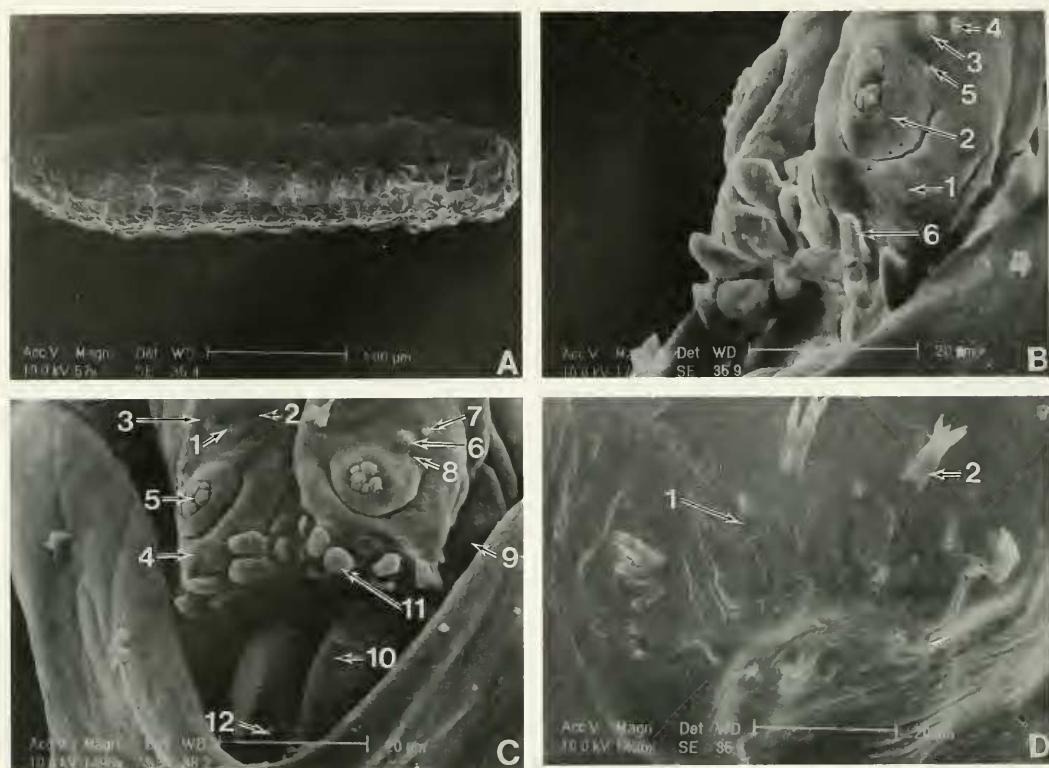
Fig. 2.   Second instar of *Neaspilota aenigma:* (A) habitus, anterior to left; (B) upper gnathocephalon, anterolateral view, 1- anterior sensory lobe, 2- terminal sensory organ, 3- lateral sensory organ, 4- supralateral sensory organ, 5- pit sensory organ, 6- integumental petal; (C) gnathocephalon, frontal view, 1- dorsal sensory organ, 2- inner, pore sensillum, 3- outer, two pore sensilla, 4- anterior sensory lobe, 5- terminal sensory organ, 6- lateral sensory organ, 7- supralateral sensory organ, 8- pit sensory organ, 9- stomal sense organ, 10- mouth hook, 11- integumental petal, 12- median oral lobe; (D) posterior spiracular plate, 1- rima, 2- interspiracular process.

mouth hook (Fig. 2B-6, C-11); median oral lobe present (Fig. 2C-12); oral ridges not seen; anterior thoracic spiracle with three oblong papillae; lateral spiracular complexes not seen; caudal segment with two stelex sensilla dorsolaterad and ventrolaterad of posterior spiracular plate (not shown); posterior spiracular plate bears three ovoid rimae, ca. 0.014 mm long (Fig. 2D-1), and four interspiracular processes, each with one to four branches, longest measuring 0.011 mm (Fig. 2D-2); intermediate sensory complex consists of a stelex sensillum and a medusoid sensillum.

The habitus of the second instar of *N. aenigma* is more like *N. wilsoni* (Goeden and Headrick 1999) and *N. signifera* (Goe-

den 1999) than the barrel-shaped second instar of *N. viridescens* (Goeden and Headrick 1992). Like both *N. viridescens* (Goeden and Headrick 1992) and *N. wilsoni* (Goeden and Headrick 1999), but not *N. signifera* (Goeden 1999), the dorsal sensory organ of *N. aenigma* is not well defined in the second instar (Fig. 2C-1). The integumental petals of the second instars of all four species are papilliform, and about eight in number above each mouth hook in *N. aenigma* (Fig. 2B-7, C-10), seven in *N. wilsoni* (Goeden and Headrick 1999), six in *N. viridescens* (Goeden and Headrick 1992), and four in *N. signifera* (Goeden 1999); whereas, in the first instars these structures are broad, flattened, and paired (Goeden

and Headrick 1992, 1999). Finally, the interspiracular processes each bear one to four branches (Fig. 2D-2), not two to four branches like *N. signifera* (Goeden 1999), nor five to nine branches like those of *N. viridescens* (Goeden and Headrick 1992), or two to six branches like those of *N. wilsoni* (Goeden and Headrick 1999).

Third instar: Whitish to pale yellow, with posterior spiracular plate dark brown to black, elongate-cylindrical, tapering anteriorly; posterior spiracular plate on caudal segment flattened and upturned dorsally ca. 60° (Fig. 3A), minute acanthae circumscribe anterior, pleural, and posterior areas of thoracic and abdominal segments (Fig. 3B-1, D-1), acanthae more numerous on posterior body segments; gnathocephalon conical; dorsal sensory organ a well-defined, circular, flattened pad (Fig. 3B-2, C-1) surrounded at margins by several pit sensilla (Fig. 3B-3); anterior sensory lobe (Fig. 3B-4, D-2) bears the terminal sensory organ (Fig. 3B-5, C-2, D-3), pit sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), and supralateral sensory organ (Fig. 3C-5); six, small upper and two, large lower, papilliform, integumental petals in separate, parallel rows above each mouth hook (Fig. 3B-6, C-6); at least seven, probably eight, oral ridges lateral to mouth hooks, oral ridges dentate along ventral margins (Fig. 3B-7, C-7); stomal sense organ prominent ventrolaterad of anterior sensory lobe (Fig. 3B-8, C-8); mouth hook tridentate (Fig. 3B-9, D-4, E-1); median oral lobe laterally flattened (Fig. 3B-10, D-5, E-2); prothorax smooth, not circumscribed by minute acanthae; anterior thoracic spiracle on posterior margin of prothorax bears three oblong papillae; metathoracic lateral spiracular complex consisting of two verruciform sensilla (Fig. 3F-1), one each, above and below spiracle (Fig. 3F-2); abdominal lateral spiracular complex consists of a spiracle (Fig. 3G-1) anterior to vertical row of three verruciform sensilla (Fig. 3G-2); caudal segment broadly circumscribed by minute acanthae (Fig. 3H); stelex sensilla (not shown) dorsolaterad, laterad, and ventrolaterad of posterior spiracular plate; each posterior spiracular plate bears three ovoid rimae, ca. 0.017 mm in length (Fig. 3H-1), and four interspiracular processes (Fig. 3H-2), each with one to three, simple, pointed branches, longest branch measuring 0.011 mm; intermediate sensory complex with a medusoid sensillum and a stelex sensillum ringed by four to five, hemispherical minute acanthae and a short, upright, apically rounded acanthus.

The habitus of the third instar of *N. signifera* generally is like that reported for *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), and *N. signifera* (Goeden 2000), except that the minute acanthae circumscribe the body segments differently. In *N. aenigma* the anterior, pleural, and posterior areas of each segment are circumscribed; in *N. signifera* the anterior part of each segment is circumscribed; in *N. wilsoni,* all intersegmental areas and all abdominal segments except the pleural areas are circumscribed; and in *N. viridescens,* the intersegmental areas are free of acanthae. Unlike *N. viridescens* (Goeden and Headrick 1992) and *N. wilsoni* (Goeden and Headrick 1999), but like *N. signifera* (Goeden 1999), the dorsal sensory organ is well-defined, but flattened, not dome-shaped in the third instar of *N. aenigma* (Fig. 3B-2, C-1). In the second instar of *N. wilsoni* (Goeden and Headrick 1999) and *N. signifera* (Goeden 2000), the dorsal sensory organ is both prominent and dome-shaped, as it is in the first instar of all congeners except *N. signifera,* where it was obscured from view and could not be examined for comparison (Goeden 2000).

Additional similarities and differences were noted. The integumental petals in the third instar of all four congeners are papilliform and arranged in a double row above each mouth hook (Goeden and Headrick 1992, 1999; Goeden 2000; Fig. 3B-6, C-7). The stomal sense organs of the third instars of all three species are especially well-developed compared to earlier instars and bear differing sensory structures, described
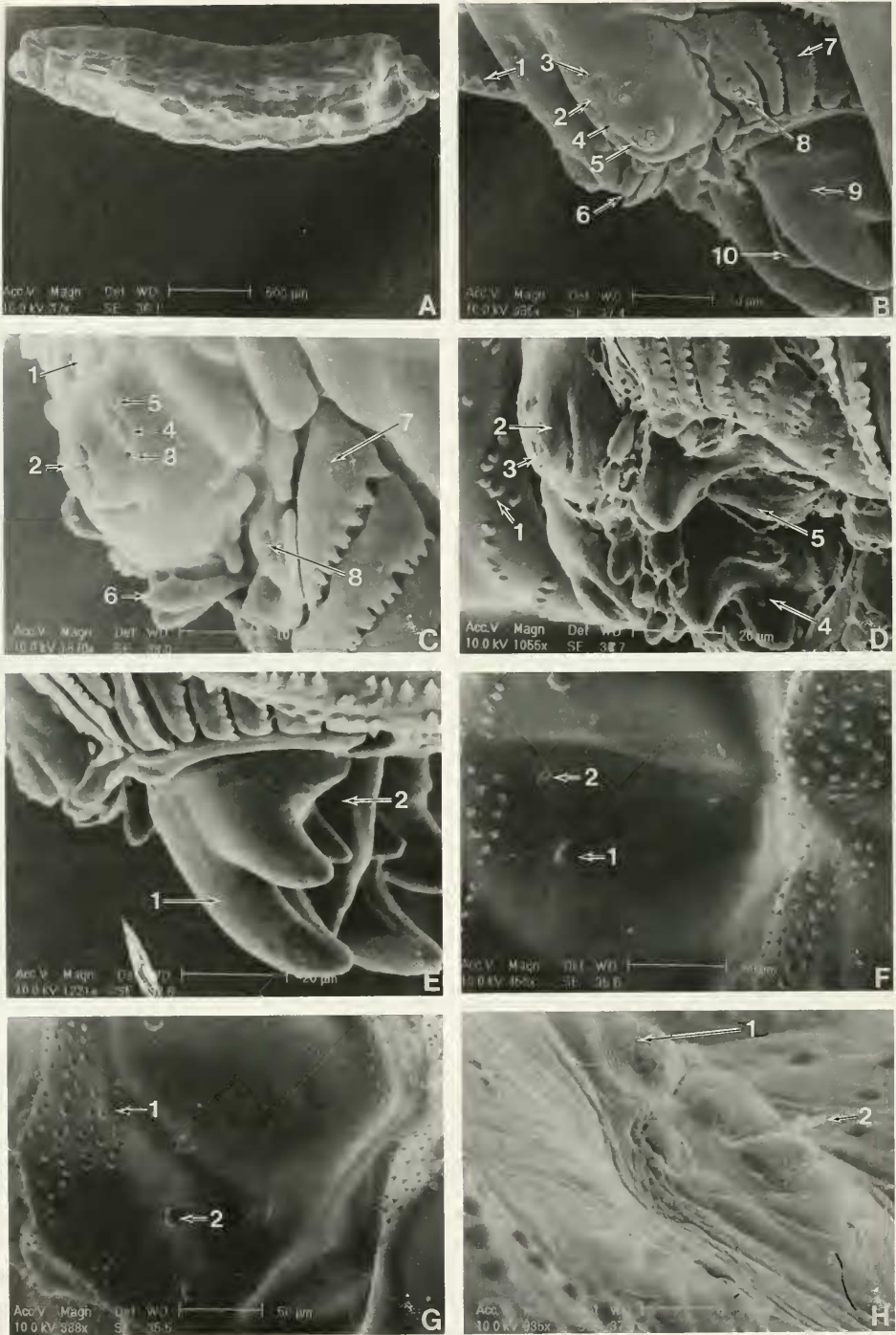
Fig. 3.   Third instar of *Neaspilota aenigma:* (A) habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1- minute acanthae, 2- dorsal sensory organ, 3- pit sensilla, 4- anterior sensory lobe, 5- terminal sensory organ, 6- integumental petal, 7- oral ridge, 8- stomal sense organ, 9- mouth hook, 10- median oral lobe; (C) anterior sensory lobe, lateral view, 1- dorsal sensory organ, 2- terminal sensory organ, 3- pit sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- integumental petal, 7- oral ridge, 8- stomal sense organ; (D) gnathocephalon, ventrolateral view, 1- minute acanthae, 2- anterior sensory lobe, 3- terminal sensory organ,

as several cone-shaped sensilla in *N. viridescens* (Goeden and Headrick 1992); as papilliform and pit-type in *N. wilsoni* (Goeden and Headrick 1999); as verruciform or "compound verruciform" in *N. signifera* (Goeden 2000), and verruciform and pit-type in *N. aenigma* (Fig. 3B-8, C-8). The third instars of all four species of *Neaspilota* examined to date have oral ridges with dentate ventral margins characteristically arranged in vertical series ventrad of the anterior sensory lobe, also reported in the second instars of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), and *N. signifera* (Goeden 2000). The oral ridges number seven or eight in the third instar of *N. aenigma* (Fig. 3B-7, C-7), but six in the second and third instars of the other three congeners examined to date. Further comparison with additional congeneric species may show the appearance and arrangement of these oral ridges to be a generic character; however, the present study also shows that the oral ridges may or may not vary in number among different congeneric species. The third instars of *Trupanea imperfecta, T. jonesi, T. nigricornis, T. pseudovicina, T. signata,* and *T. wheeleri* also bear serrated oral ridges (Goeden and Teerink 1997a, 1998, 1999b; Goeden et al. 1998a; Knio et al. 1996; Teerink and Goeden 1999), but these oral ridges appear to be fewer in number, and are not arranged in a more or less regular, vertical row laterad of the oral cavity, as in *Neaspilota*. The mouth hooks of the third instars of *N. aenigma, N. signifera,* and *N. viridescens* are tridentate (Fig. 3D-4, E-1, Goeden and Headrick 1992, Goeden 2000); whereas, those of the third instar of *N. wilsoni* are bidentate (Goeden and Headrick 1999). Such interspecific differences in dentation are supported by our findings that the mouth hooks of third- instar *Trupanea vicina* are bidentate; whereas, those of 12 other congeners examined from California are tridentate (Goeden and Teerink 1999c and citations therein).

The number and appearance of the stelex sensilla surrounding the posterior spiracular plates differ among the *Neaspilota* species examined to date. Goeden and Headrick (1999) speculated that the 10 stelex sensilla reported by Goeden and Headrick (1992) to surround both posterior spiracular plates of the first instar of *N. viridescens* were suspect in number. These number only four (two laterad of each plate) in *N. wilsoni* (Goeden and Headrick 1999) and *N. aenigma* (see description above), but unfortunately were not observed with *N. signifera* (Goeden 2000). Because my unpublished count for *N. appendiculata* Freidberg and Mathis is the same as *N. wilsoni* and *N. aenigma,* the count for *N. viridescens* by Goeden and Headrick (1992) is rendered even more suspect. This count of stelex sensilla remains at four in the second instars of *N. aenigma* (see above description) and *N. appendiculata* (unpublished data), but increases to six in third instars of *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (see above description), and *N. appendiculata* (unpublished data). These stelex sensilla also show inter-instar (intraspecific) and interspecific differences in the incidence and appearance of the minute acanthae that may ring them basally, but this was not recognized, studied and recorded by my coworkers and me until recently (Goeden 2000, above, and unpublished data).

Puparium: Mostly white to yellow, with posterior two to three segments grayish to

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4- mouth hook, 5- median oral lobe; (E) mouth hooks and median oral lobe, posterior lateral view, 1- mouth hook, 2- median oral lobe; (F) metathoracic lateral spiracular complex, 1- verruciform sensillum, 2- spiracle; (G) first abdominal spiracular complex, 1- spiracle, 2- verruciform sensillum; (H) posterior spiracular plate, 1- rima, 2- interspiracular process.

blackened posteriorly, broadly ellipsoidal and smoothly rounded at both ends (Fig. 4A), minute acanthae circumscribe anterior, pleural, and posterior areas of body segments; anterior end bears the invagination scar (Fig. 4B-1) and anterior thoracic spiracles (Fig. 4B-2); caudal segment circumscribed by minute acanthae, six stelex sensilla, dorsolaterad, laterad, and ventrolaterad of posterior spiracular plates; posterior spiracular plate bears three broadly elliptical rimae (Fig. 4C-1), and four interspiracular processes, each with one to three branches (Fig. 4C-2); intermediate sensory complex consists of a medusoid sensillum and a stelex sensillum. Forty-two puparia averaged 2.7 ± 0.04 (range, 2.13–3.13) mm in length; 1.10 ± 0.02 (range, 0.78–1.35) mm in width.

DISTRIBUTION AND HOSTS

Freidberg and Mathis (1986) described the distribution of *N. aenigma* as "Southwestern United States and northern Mexico (Colorado westward to California, southward through Texas to Sonora Mexico)." Foote et al. (1993) mapped the distribution to include multiple collection records from Arizona, California, New Mexico, and Texas, along with an additional single collection record from Colorado.

New light is shed on the hosts of *N. aenigma* by our repeated sole rearings of adults from flower heads of *Erigeron divergens* during the course of these studies. Adults were also reared from flower heads of *E. foliosus* Nuttall, within which *N. aenigma* co-occurs in symphagy (Goeden 1997) with *Procecidochares* n. sp. nr. *minuta* Snow and *Trupanea wheeleri* Curran; this symphagy is one reason why *N. aenigma* was not studied in the latter host during the present study. These two plants in the subtribe Asterinae of the tribe Astereae in the Asteraceae represent new host-plant species, genus, and subtribe records for *N. aenigma* (Freidberg and Mathis 1986, Goeden 1989). Freidberg and Mathis (1986, p. 9) reported this tephritid from *Machaer-*
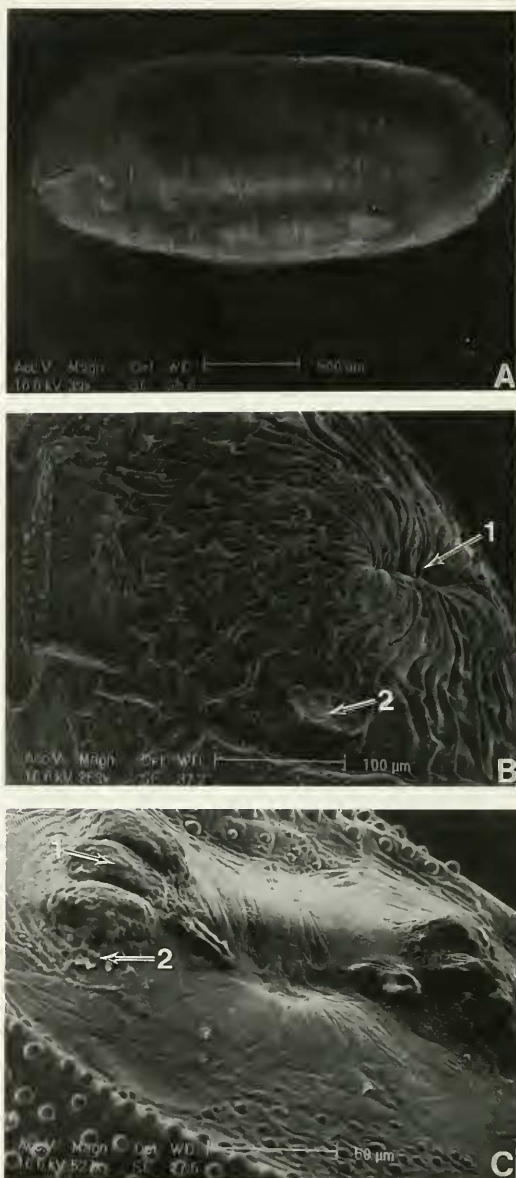

Fig. 4. Puparium of *Neaspilota aenigma:* (A) habitus, anterior to right; (B) anterior end, 1- invagination scar, 2- anterior thoracic spiracle; (C) caudal segment, 1- rima, 2- interspiracular process (both partly obscured by debris).

anthera pinnatifida (Hooker) var. *Gooddingii* (Nelson) B. Turner and R. Hartman [as *Haplopappus Goodingii* (A. Nelson) Munz and I. M. Johnson] and *H. hartwegi* Blake, which they and Foote et al. (1993) termed a confirmed host and a suspected host, re-

spectively. Goeden (1989) reported *N. aenigma* from *Acamptopappus shockleyi* A. Gray and *Xylorhiza tortifolia* (Torrey and A. Gray) E. Greene var. *tortifolia* [as *Machaeranthera tortifolia* (Torrey and A. Gray) Cronquist and Keck], both high-elevation, Mojave Desert shrubs which, along with the preceding two hosts, also belong to the subtribe Solidagininae of the tribe Astereae. *Ericameria* (= *Haplopappus*) *laricifolia* (A. Gray) Shinners, also belonging to the latter subtribe, is hereby reported as another fall-blooming, Mojave Desert shrub from which *N. aenigma* has been reared in southern California. The records for single females reared from *Lessingia lemmoni* Gray in Goeden (1989), upon re-examination of these specimens, probably should refer to *N. brunneostigmata* Doane. Thus, to date, *N. aenigma* has been reported from seven plant species in six genera from two subtribes of the tribe Astereae (Bremer 1994), and is best characterized as narrowly oligophagous (Headrick and Goeden 1998).

BIOLOGY

Egg.—In three, closed, preblossom, immature flower heads of *E. divergens*, three eggs were inserted pedicel-last, one between the chaff and ovules, two within single florets, and the long axes of all three eggs were perpendicular to the receptacle (Fig. 5A). The diameters of the receptacles of these three flower heads containing eggs ranged from 2.85 to 3 mm.

Larva.—Upon eclosion, the first instars usually tunneled into an ovule, or into a corolla before entering the ovule attached basally to it (Fig. 5B). Single first instars were found feeding within each of 12, closed, preblossom or open flower heads; another preblossom head contained two first instars. The receptacles of these 13 flower heads averaged 2.6 ± 0.1 (range, 2.0–3.4) mm in diameter. An average of 2.6 ± 0.1 (range, 2–13) ovules or soft achenes was damaged in these 13 heads as the first instar tunnelled through the layer of ovules or soft achenes and parallel to and above the receptacle. No

receptacles within these 13 infested flower heads were abraded or pitted by feeding. Based on 192 (range, 105–240) as the average total number of ovules and achenes respectively counted in 35 preblossom to postblossom flower heads, about 5.9% (range, 1.9–12.4%) of the ovules in the 13 infested, preblossom flower heads were damaged by first instars.

Second instars continued feeding on ovules in preblossom flower heads or in soft achenes in open flower heads (Fig. 5C). All fed within a series of adjacent ovules/soft achenes with their bodies horizontal to and their mouthparts directed towards the receptacles, but always well above the receptacles. Receptacles of 31 flower heads containing second instars were not fed upon and averaged 2.73 ± 0.05 (range, 2.13–3.42) mm in diameter. These flower heads each contained one second instar that had destroyed an average of 33.4 ± 4.2 (range, 8–90) ovules/soft achenes, or as calculated for the preceding instar, about 22.5% (range, 12–40%) of the average total of 192 ovules/soft achenes per flower head.

Third instars initially continued to feed mainly on soft achenes horizontal to the receptacle around the periphery of post blossom flower heads; however, prior to pupariation, and before all the achenes were damaged, they proceeded to tunnel into the center of the receptacle (Fig. 5D) and sometimes continued into the peduncle (Fig. 5F). Fifty-nine flower heads that averaged 3.19 ± 0.06 (range, 2.28–4.27) mm in diameter each contained a single third instar. An average of 84.5 ± 9.1 (range, 35–180) of the soft achenes therein were damaged, or about 61% (range, 33–79%) of the average total of 192 ovules/soft achenes per flower head. Upon completing their feeding, the larvae oriented with their anterior ends directed away from the receptacles, retracted their mouthparts, and pupariated, as described for *N. signifera* (Goeden 2000) and other florivorous, noncongeneric, tephritids that do not overwinter in flower heads, e.g., *Trupanea* spp. (Headrick and Goeden 1998). No other
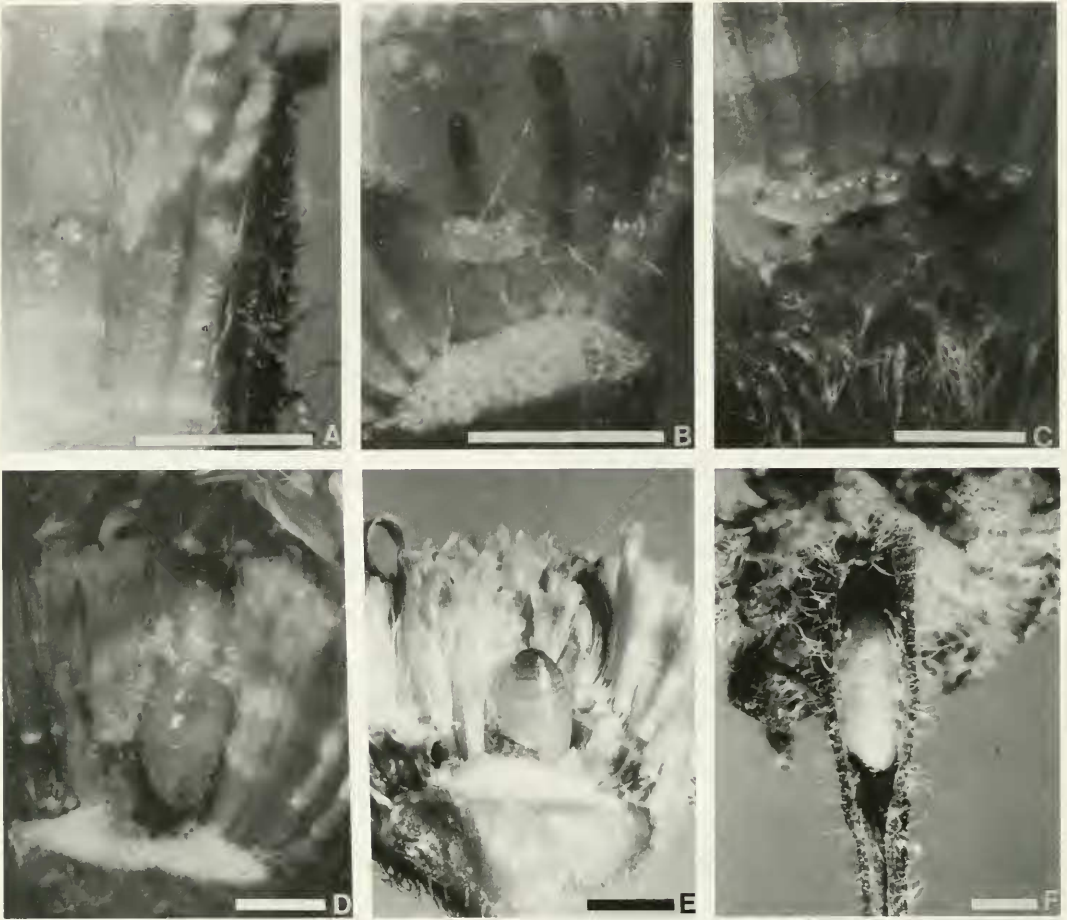
Fig. 5. Life stages of *Neaspilota aenigma* in *Erigeron* spp.: (A) egg laid between florets in preblossom flower head of *E. divergens*; (B) first instar tunneling into corolla and ovules in closed flower head of *E. divergens*; (C) second instar feeding on ovules in flower head of *E. divergens*, (D) third instar feeding on soft achenes in center of open flower head of *E. divergens*, (E) puparium sunk in receptacle of open flower head of *E. divergens*; (F) puparium in pedicel below surface of receptacle of postblossom flower head of *E. foliosus*. Lines = 1 mm.

florivorous tephritid that we have studied to date has fed as deeply into, and sometimes through, the receptacle and into the pedicel, a mode of feeding expressed to its fullest in the *Cirsium* thistle-, flower head-, peduncle-, stem- and crown-mining tephritid, *Chetostomella undosa* (Coquillett) (Steck 1984; Goeden and Ricker 1986).

Pupa.—The receptacles of 46 postblossom flower heads, each containing a single puparium (Fig. 5E), averaged 3.28 ± 0.04 (range, 2.85–4.00) mm in diameter. Seventeen of these flower heads contained an average total of 143.8 ± 3.0 (range, 120–165) soft achenes that had been damaged by larval feeding, or calculated as above, 70% (range, 54–81%) average seed predation. This mean percentage seed predation per larva per flower head is on the high side among florivorous tephritids studied by us to date (Headrick and Goeden 1998); it is exceeded only by gregarious florivorous species like *Trupanea conjuncta* (Adams) (Goeden 1987) and *T. pseudovicina* Hering (Goeden and Teerink 1998) or by species with large larvae that develop in immature

or small flower heads like *Paracantha cultaris* (Coquillett) (Cavender and Goeden 1984) and *Xenochaeta dichromata* Snow (Goeden and Teerink 1997a). The receptacles of all but one (98%) of the 46 flower heads were pitted by larval feeding. Most puparia of *N. aenigma* were found in the centers of the flower heads partly buried basally in the receptacle to a depth of 2.8 ± 0.58 (range, 0–5.4; n = 12) mm within 0.83 ± 0.06 (range, 0.57–1.14; n = 17) mm-diam pits and with their long axes perpendicular to the receptacles (Fig. 5E, F).

Adult.—Adults emerged from mature flower heads, and were long-lived under insectary conditions, as 55 unmated males averaged 48 ± 5 (range, 5–205) days, and 72 virgin females averaged 71 ± 4 (range, 5–148) days. Such lengthy longevities are commensurate with the aggregative type of life cycle described below for this tephritid, and compare favorably with average adult longevities reported for adults of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), and *N. signifera* (Goeden 2000).

The premating and mating behaviors of *N. aenigma* were not studied in the field, but were observed in petri dish arenas found to be so useful with many other noncongeneric, nonfrugivorous, tephritid species (Headrick and Goeden 1994). Premating behaviors observed with *N. aenigma* were abdominal pleural distension and side-stepping (Headrick and Goeden 1994), and wing hamation, sometimes combined with lofting 10–20° by both sexes (Headrick and Goeden 1994). However, no trophallaxis or nuptial gift presentation was noted as reported with *N. viridescens* (Goeden and Headrick 1992). Four matings (Fig. 5H, 5I) were observed that usually began during late afternoon at dusk involving three different pairs of flies that lasted an average of 190 (range, 120–265) min, somewhat shorter than, but still comparatively long, like the average durations of 235 min. reported for *N. wilsoni* (Goeden and Headrick 1999), 238 min. reported for *N. signifera*

(Goeden 1999), and 5.3 h reported for *N. viridescens* (Goeden and Headrick 1992). No post-copulatory behavior reminescent of the mate guarding observed with *N. signifera* (Goeden 2000), *Dioxyna picciola* (Bigot) (Headrick et al. 1996), and *Euaresta stigmatica* Coquillett (Headrick et al. 1995) was observed with *N. aenigma*.

Seasonal history.—The life cycle of *N. aenigma* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the long-lived adults probably are the principal overwintering stage. Come late spring (April–May), surviving, overwintered adults aggregate on preblossom *Erigeron divergens*, *Acamptopappus shockleyi*, *Xylorhiza tortifolia*, and probably additional, as-yet-unidentifed, spring blooming hosts for mating and oviposition. The F_1 adults emerge in late spring (May) and early summer (June), mate, and complete a summer F_2 generation on late-flowering *E. divergens* growing at higher elevations along with *E. foliosus* and probably other, as yet unidentified, alternate hosts (July–August), and another fall F_3 generation in late-flowering (September–October), Mojave Desert hosts, e.g., *Ericameria laricifolia*. Some of these F_2 and probably all F_3 adults overwinter, and those that survive aggregate the next spring (April–May) on preblossom host plants to continue the life cycle.

Natural enemies.—Many specimens of *Pteromalus* sp. (Hymenoptera: Pteromalidae) were reared from puparia of *N. aenigma* as its principal, solitary, larval-pupal endoparasitoid. Similarly, many specimens of an unidentified Braconidae were reared from flower heads of *Erigeron foliosus* infested with *N. aenigma*, and a single male was reared separately from a third instar, confirming this host/parasitoid relationship. Also reared from infested flower heads as probable parasitoids were a single specimen of Eulophidae, and several individuals of *Colotrechnus* sp.

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Literature Cited

Bremer, K. 1994. Asteraceae Cladistics & Classification. Timber Press, Inc. Portland, Oregon.

Cavender, G. L. and R. D. Goeden. 1982. Life history of *Trupanea bisetosa* (Diptera: Tephritidae) on wild sunflower in southern California. Annals of the Entomological Society of America 75: 400–406.

Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993. Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico. Cornell University Press, Ithaca, New York.

Freidberg, A. and W. N. Mathis. 1986. Studies of Terelliinae (Diptera: Tephritidae): a revision of the genus *Neaspilota* Osten Sacken. Smithsonian Contributions to Zoology 439: 1–75.

Goeden, R. D. 1987. Life history of *Trupanea conjuncta* (Adams) on *Trixis californica* Kellogg in southern California (Diptera: Tephritidae). The Pan-Pacific Entomologist 63: 284–291.

———. 1989. Host plants of *Neaspilota* in California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 91: 164–168.

———. 1997. Symphagy among florivorous fruit flies (Diptera: Tephritidae) in southern California. Chap. 3 *In:* K. Dettner, G. Bauer, and W. Volkl (eds.). Vertical Food Web Interactions: Evolutionary Patterns and Driving Forces. Ecological Studies 130: 39–52. Springer-Verlag, Heidelberg, Germany.

———. 2000. Life history and description of immature stages of *Neaspilota signifera* (Coquillett) (Diptera: Tephritidae) on *Hemizonia pungens* (Hooker and Arnott) Torrey and A. Gray (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 102: 69–81.

Goeden, R. D. and D. H. Headrick. 1992. Life history and descriptions of immature stages of *Neaspilota viridescens* Quisenberry (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 94: 59–77.

———. 1999. Life history and description of immature stages of *Neaspilota wilsoni* Blanc and Foote (Diptera: Tephritidae) on *Hazardia squarrosa* (Hooker and Arnott) E. Greene (Asteraceae). Proceedings of the Entomological Society of Washington 101: 897–909.

Goeden, R. D. and D. W. Ricker. 1986. Phytophagous insect faunas of the two most common native *Cirsium* thistles, *C. californicum* and *C. proteanum*, in southern California. Annals of the Entomological Society of America 79: 953–962.

Goeden, R. D. and J. A. Teerink. 1997a. Life history and description of immature stages of *Xenochaeta dichromata* Snow (Diptera: Tephritidae) on *Hieracium albiflorum* Hooker in central and southern California. Proceedings of the Entomological Society of Washington 99: 597–607.

———. 1997b. Life history and description of immature stages of *Trupanea signata* Foote (Diptera: Tephritidae) on *Gnaphalium luteo-album* L. in southern California. Proceedings of the Entomological Society of Washington 99: 748–755.

———. 1998. Life history and description of immature stages of *Trupanea pseudovicinia* Hering (Diptera: Tephritidae) on *Porophyllum gracile* Bentham (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 100: 361–372.

———. 1999a. Life history and description of immature stages of *Trupanea arizonensis* Malloch (Diptera: Tephritidae) on *Trixis californica* Kellog var. californica (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 101: 75–85.

———. 1999b. Life history and description of immature stages of *Trupanea wheeleri* Curran (Diptera: Tephritidae) on Asteraceae in southern California. Proceedings of the Entomological Society of Washington 101: 414–427.

———. 1999c. Life history and description of immature stages of *Trupanea vicina* (Wulp) (Diptera: Tephritidae) on wild and cultivated Asteraceae in southern California. Proceedings of the Entomological Society of Washington 101: 742–755.

Goeden, R. D., J. A. Teerink, and D. H. Headrick. 1998a. Life history and description of immature stages of *Trupanea jonesi* Curran (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 100: 126–140.

———. 1998b. Life history and description of immature stages of *Trupanea actinobola* (Loew)

(Diptera: Tephritidae) on *Acamptopappus sphaerocephalus* (Harvey and Gray) Gray (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 100: 674–688.

Headrick, D. H. and R. D. Goeden. 1994. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. Studia Dipterologica 1(2): 194–252.

———. 1998. The biology of nonfrugivous tephritid fruit flies. Annual Review of Entomology 43: 217–241.

Headrick, D. H., R. D. Goeden and J. A. Teerink. 1995. Life history and description of immature stages of *Euaresta stigmatica* Coquillett (Diptera: Tephritidae) on *Ambrosia* spp. (Asteraceae) in southern California. Annals of the Entomological Society of America 88: 58–71.

———. 1996. Life history and description of immature stages of *Dioxyna picciola* (Bigot) (Diptera: Tephritidae) on *Coreopsis* spp. (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 98: 332–349.

Hickman, J. C. (ed.) 1993. The Jepson Manual. University of California Press. Berkeley and Los Angeles.

Knio, K. M., R. D. Goeden and D. H. Headrick. 1996. Descriptions of immature stages of *Trupanea nigricornis* and *T. bisetosa* (Diptera: Tephritidae) from southern California. Annals of the Entomological Society of America 89: 1–11.

Steck, G. J. 1984. *Chaetostomella undosa* (Diptera: Tephritidae): Biology, ecology, and larval description. Annals of the Entomological Society of America 77: 669–678.

Teerink, J. A. and R. D. Goeden. 1998. Description of the immature stages of *Trupanea conjuncta* (Adams). Proceedings of the Entomological Society of Washington 100: 431–438.

———. 1999. Description of the immature stages of *Trupanea imperfecta* (Coquillett). Proceedings of the Entomological Society of Washington 101: 225–232.